

TIME BUDGET OF BREEDING GADWALLS

THOMAS J. DWYER

Time budget studies have been made of birds as diverse as blackbirds (Orians 1961), wrens (Verner 1965), hummingbirds (Wolf and Hainsworth 1971) and finches (Schartz and Zimmerman 1971) but few accounts of duck time budgets have been published. Tamisier (1972) recently studied the activity rhythm of wintering European Green-winged Teal (*Anas crecca*). Klima (1966) described the activity rhythm of the European Pochard (*Aythya ferina*) and Folk (1971) added data on the Tufted Duck (*A. fuligula*). These authors were mainly concerned with detecting diurnal or nocturnal activity patterns and did not discuss how the division of time among various activities related to the reproductive strategy of the species. Titman (1973), however, did present data on the daily routine of Mallard (*Anas platyrhynchos*) pairs during the breeding season.

Dwyer (1974) studied the social behavior of the Gadwall (*Anas strepera*) and the importance of foraging activities to its territorial behavior. This paper will elaborate on that concept and demonstrate how the remaining activities relate to the reproductive strategy of pairs.

STUDY AREA AND METHODS

Data were gathered in 1973 in the glaciated prairie region of south-central North Dakota. The study area, 9.6 km south of Medina in west-central Stutsman Co., consists of rolling hills interspersed with small undrained depressions containing wetlands of various sizes and types. The number of wetland basins per square km ranges from 2 to 12 and they average 1.6 ha in size. Approximately 40% of the uplands is pasture and forage crops and 60% is small grain crops.

Gadwall pairs or lone males were observed with a 20× spotting scope or 7 × 35 binoculars during one-hour intervals in the daylight hours of April, May, and June, 1973. A metronome timing device (Wiens et al. 1970) set at a 15-sec interval was used to give a time base for recording activities. Each time the tone sounded the activity of both members of a pair or lone male was recorded. Two, one-hour sampling periods were picked at random during 3 separate time periods of the day, 06:00–11:00, 11:00–16:00, and 16:00–21:00 hours. I attempted to observe a pair for one full hour in each of the 3 time periods each day. Inclement weather, farming activities, or unavailable birds prevented fulfillment of this goal approximately one-half of the time. Observations were made on a variety of pond types over a 41.4 sq km area. An energy budget was constructed for male Gadwalls by extrapolation from time budget data in order to examine the costs of defense of the female during the breeding season.

For purposes of data analysis I split the breeding season into 3 phases: spring arrival, prenesting, and laying. Pairs in flocks were considered to be in the spring arrival

phase until the second week of May. After that date, pairs showing intraspecific intolerance and obviously not in flock situations were judged to be in the prenesting phase. Gadwalls show more synchrony in the start of nesting than most ducks (Duebbert 1958, Oring 1969). Nest records and brood observations on the study area in 1972 and 1973 showed that most hens began nesting the last week of May. Thus, I could be reasonably sure that birds were in the prenesting phase until the latter part of May. Observations were made of 2 pairs in the laying phase. I could identify each drake by plumage characteristics and I confirmed that the females were laying by watching them fly to the nest while the drake remained on the pond alone.

I did not use data resulting from less than 30 min of continuous observation. Thirteen hours of observations made during the spring arrival period were not picked at random. Data for the prenesting and laying phase totaled 34.8 and 23.4 hours, respectively. Six hours of data were also gathered on lone males waiting for their laying females. Paired or unpaired *t* tests, as appropriate, were used to test for differences between means and statistical significance was inferred when $P < 0.05$.

The activities of the birds were categorized as follows:

Feeding.—This activity was recorded only when a bird was actually ingesting food obtained by surface or subsurface feeding. Birds sometimes swam short distances and immediately began feeding again. The time involved in changing location was coded as locomotor activities.

Resting.—This activity included sleeping and loafing on the water or shore of a pond.

Locomotor activities.—Swimming and walking on the shore of a pond or in shallow water were included in this category.

Comfort movements.—This category included all activities involved with body maintenance such as preening and bathing.

Threat postures.—Open-bill threat postures by males and Chin-lift postures (Lorenz 1953) by pairs or males involved in intraspecific encounters were recorded in this category.

Three-bird chases.—This activity involved aerial pursuit of a paired female by a paired male followed by the female's mate.

Alert.—Pairs normally stop all activities and assume a head upright posture when they are disturbed by other birds, farm machinery, or road vehicles. This behavior is common in a mated drake during prenesting and laying when his female is feeding, even when a disturbance is not present.

Out-of-sight.—Pairs or lone males were occasionally shielded from view by vegetation for short periods of time. Calculations of percentage of time spent in various activities were based on the amount of time birds were actually observed.

RESULTS

Seasonal activity of pairs.—The average amount of time paired Gadwalls spent in various activities during the spring arrival, prenesting, and laying phases is presented in Fig. 1. Females spent most of their time feeding during all 3 phases of the breeding season. During the spring arrival phase, feeding rates were remarkably similar between members of pairs (Fig. 1). Male feeding rates began to decline as soon as birds became

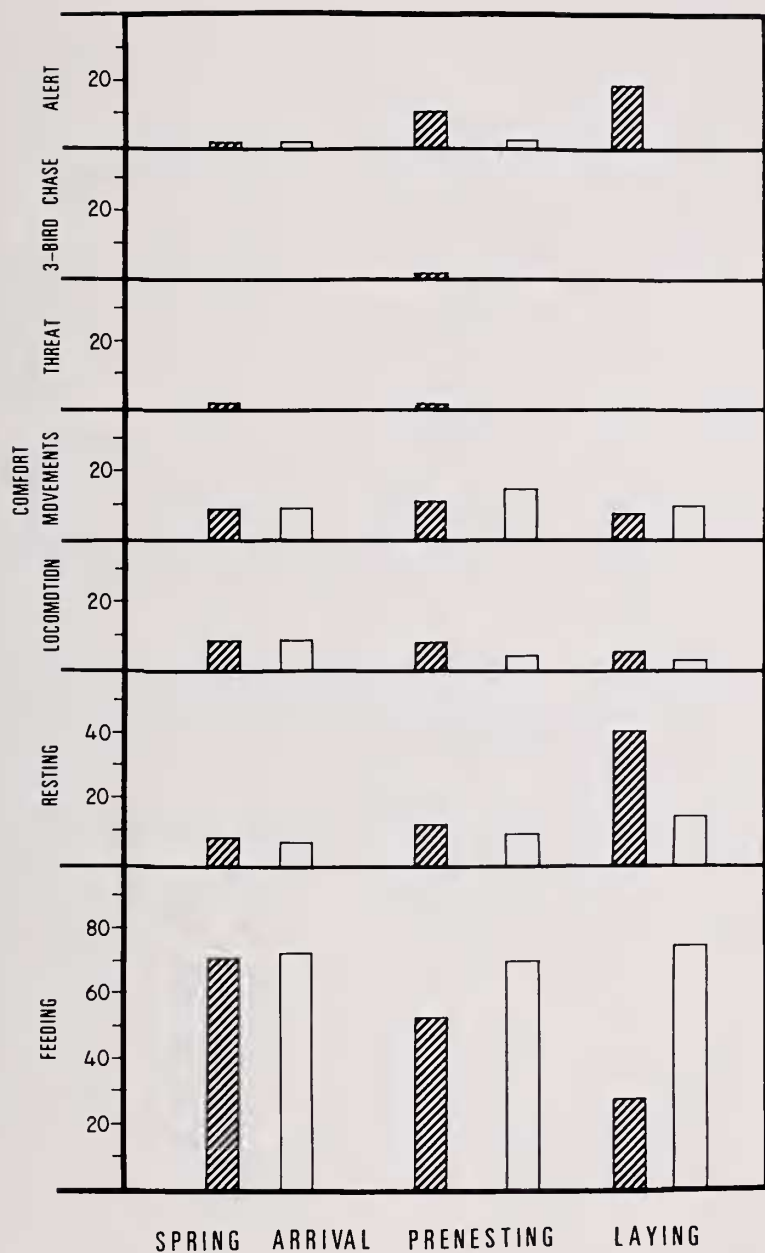


FIG. 1. Percent of time spent in various activities by pairs of Gadwalls. Males are indicated by crosshatching, females are unshaded. Percentages of less than 0.5 are not shown.

established on activity centers during the prenesting phase. Feeding rates for prenesting and laying females were significantly greater than for their mates. The average length of feeding bouts (the length of time during which only feeding activities were coded) for females averaged 6.9, 3.3, and 7.2 min during spring arrival, prenesting and laying, respectively, whereas male feeding bouts averaged 6.6, 1.9, and 0.9 min during the same time periods.

Time spent in resting activities was relatively constant for males and females during the spring arrival and prenesting phase but increased markedly in the males during the laying phase. Comfort movements consumed relatively constant amounts of time for males and females during all 3 phases. Locomotor activities consumed a smaller amount of time for both sexes as the season progressed.

The percentage of time paired males spent in threat postures decreased from 1.4% during spring arrival to 0.7% during prenesting and to 0.4% during laying. This decrease reflects the isolation pairs maintain from other pairs and unmated drakes as the season progresses. The amount of time spent by paired males in 3-bird flights, however, reached a maximum during prenesting and was significantly greater in this phase than in the laying phase.

Males and females spent similar amounts of time in an alert posture during the spring arrival phase. During prenesting and laying, paired males spent a significantly greater amount of time in an alert posture than did females. Males also spent a significantly greater amount of time in an alert posture during laying than during prenesting.

Daily activity patterns of pairs.—If the data are partitioned among the 3 daily time periods for the prenesting and laying phases, relatively few hours are available for analysis in each period. However, some general trends are evident. Neither males nor females changed feeding rates significantly during the day. However, female feeding rates were significantly greater than their mates regardless of the time of day. Male and female resting activities increased during the midday hours. Locomotor activities consumed the least proportion of the time in the evenings for females while no similar trend was noted for males in this activity. Comfort movements were relatively constant for females during laying but were highest in the morning during prenesting. No general pattern of comfort movements could be determined for males. Agonistic behavior or alert postures by males did not depend on the time of day but rather on the presence of other birds on the same pond or nearby farming operations.

Activities of lone males.—Drakes fed 27% of the time while with their hens but increased feeding rates to 36% of the time when they were alone.

TABLE 1
ESTIMATED ENERGY BUDGET OF MALE GADWALLS DURING 3 PHASES OF THE BREEDING SEASON

Activity	Spring Arrival		Prenesting		Laying	
	% day	Cost (kcal/bird per day)	% day	Cost (kcal/bird per day)	% day	Cost (kcal/bird per day)
Resting	5.83	4.41	9.85	7.46	28.35	21.47
Feeding	50.69	95.98	37.91	71.78	19.22	36.39
Locomotion	6.14	9.30	5.84	8.85	4.20	6.36
Comfort movements	6.26	7.11	8.33	9.46	5.38	6.11
Threat postures	0.97	2.20	0.49	1.11	0.31	0.70
3-bird chase	0.02	0.17	0.53	4.66	0.18	1.58
Alert	0.92	1.04	7.88	8.95	13.19	14.98
Nighttime	29.17	44.18	29.17	44.18	29.17	44.18
Total	100.00	164.39	100.00	156.45	100.00	131.77

Locomotor activities by drakes increased significantly from 6% to 15% when their females were absent. Drakes also spent significantly less time in the alert posture while alone than when they were with their females (5% versus 19%).

Energy budget of male Gadwalls.—Using the equation given by Lasiewski and Dawson (1967) for non-passerines, the standard metabolic rate for Gadwall males was computed as 76.7363 kcal/bird per day (using a mean weight of 0.955 kg taken from an April and May trapped sample of 7 males). The data in Fig. 1 are based on the percentage of daytime observation time and must be corrected by multiplying by 70.83% for the 7 hours of nighttime when no data were taken.

To convert the time budget data to an energy budget, several assumptions must be made. Feeding was given a value of 2.5 times resting because Gadwalls usually feed on or under the surface of the water while swimming. Locomotion was assumed to demand twice the standard metabolic rate (Prange and Schmidt-Nielson 1970) and comfort movements were given a value of 1.5 times the standard rate. Threat was given a value of 3 times resting because Gadwall males usually perform threat displays while swimming. Orians (1961) estimated the metabolic cost of displays of blackbirds to be 2 times resting. Three-bird chases were given a value of 11.6 times resting, based on Prange and Schmidt-Nielson's (1970) estimate

of the maximum sustained metabolic rate of a flying Mallard. A Gadwall drake's metabolism while involved in a vigorous 3-bird chase must be close to that value. Alert was given a value of 1.5 times resting. Night-time activity was assumed to have the same energy cost as daytime locomotion because Gadwalls are active at night and are known to feed actively at times (Swanson and Sargeant 1972). The estimated energy budget for male Gadwalls during the spring arrival, prenesting, and laying phases of the breeding season is given in Table 1. These data should be viewed as a rough approximation since the effects of temperature on metabolic rate were not taken into consideration.

DISCUSSION

Pairs establish an activity center on a pond during the prenesting phase and spend virtually all the daylight hours of each day at this location until nesting begins (Gates 1958, Dwyer 1974). Paired Gadwall drakes show 2 types of defense against intruders in their activity centers (Dwyer 1974). The response toward an unpaired male or males who attempt to court his female takes the form of the Chin-lift posture or open-bill threat display. The Mutual Chin-lift posture of the pair preceded by Inciting by the female is also common in this situation. This is usually sufficient to cause an unpaired male to leave the activity center. If he persists, he will be attacked by the paired male and driven away. Paired males react to other pairs nearing the activity center by instigating a 3-bird chase. Females of pairs are vigorously chased for periods of up to 1 min and over linear distances of 1.6 km.

Competition for activity centers becomes intense during the first part of May. Each pair attempts to gain possession of an area where the female can localize her activities, begin to feed intensively, and build up her metabolic reserves for nesting (Dwyer 1974). Apparently other pairs are able to recognize potentially fertile areas which are at times in short supply. I have seen the drake of an established pair chase the same pair away as many as 6 times before the intruding pair moved on. The time spent by paired Gadwall males in 3-bird chases declined significantly from 0.7% during the prenesting phase to 0.3% of the time during laying. Thus, the maximum effort toward territorial defense is expended to establish a pair on an activity center before laying is initiated. Milne (1974) postulated that the feeding efficiency of the female European Eider (*Somateria mollissima*), prior to laying, was a very important determinant of her ability to breed successfully. He also stated that the constant attentiveness of the paired male was important in allowing the female to increase her food intake.

Costs of defense.—Because unpaired drakes are not competing for activity centers it seems logical in terms of energetics for a paired male to spend less effort defending against them than against another pair. Thus, threat postures suffice. Other pairs, however, could compete directly for the activity center and thus must be driven completely away. Similarly, Wolf and Hainsworth (1971) found different modes of defense in tropical hummingbirds depending on the position of the intruder in the hierarchy of competitors.

Paired males expend a relatively large amount of energy during prenesting maintaining isolation for their females in activity centers (Table 1). They are able to do this even though feeding for less time than during spring arrival, probably because of increasing food resources due to higher ambient temperatures and longer photoperiod. Verner (1965) showed that male Long-billed Marsh Wrens (*Telmatodytes palustris*) spent proportionally less time feeding as the season progressed because of increasing temperature and photoperiod. Feeding rates of males whose females are laying can drop even further because less energy is required for defense at that time. Thus, it appears economically feasible in terms of time and energy for paired males to protect their females and thereby maintain exclusive feeding areas for their use.

Females obviously need to ingest a tremendous amount of food to maintain themselves as well as mobilize the energy needed to produce a clutch averaging over 9 eggs. King (1973) estimated that egg production in ducks required an increase of 50–70% above the daily energy intake needed for the maintenance level of metabolism. Thus, their feeding rates must remain high during prenesting and laying. Differences in availability of foods in different ponds could change feeding rates to some extent, but the pattern described above probably would remain the same.

SUMMARY

Time budgets for pairs of Gadwalls during the breeding season were calculated based on 71.2 hours of observation. Feeding occupied the greatest proportion of the time of female Gadwalls during the spring arrival, prenesting, and laying phases of the breeding season. Feeding rates for prenesting and laying females were significantly greater than for their mates regardless of the time of day. The percentage of time paired males were involved in agonistic encounters other than 3-bird chases decreased from 1.4% during spring arrival to 0.4% during laying. Paired males, however, spent a maximum amount of time in 3-bird chases during the prenesting phase. Feeding rates did not change significantly for males or females during the day in the prenesting or laying phase.

Gadwall drakes apparently use more energy defending their females from the approach of pairs than from unmated drakes because pairs could directly compete for an activity center. Mated drakes help assure the reproductive output of the pair

by maintaining an exclusive feeding area for the female before and during the time of egg formation.

ACKNOWLEDGMENTS

D. Alan Davenport wrote the computer program to summarize the data. I especially thank Douglas H. Johnson for editorial and statistical advice. Gary L. Krapu and George A. Swanson reviewed the manuscript. The Bioelectronics Laboratory of the James Ford Bell Museum of Natural History, University of Minnesota, constructed the metronome timing device.

LITERATURE CITED

- DUEBBERT, H. F. 1958. Island nesting of the Gadwall (*Anas strepera*) in North Dakota. M.A. thesis, Univ. of Missouri, Columbia.
- DWYER, T. J. 1974. Social behavior of breeding Gadwalls in North Dakota. *Auk* 91:375-386.
- FOLK, C. 1971. A study on diurnal activity rhythm and feeding habits of *Aythya fuligula*. *Acta Sc. Nat. Brno*. 5:1-39.
- GATES, J. M. 1958. A study of the breeding behavior of the Gadwall in northern Utah. M.S. thesis, Utah State Univ., Logan.
- KING, J. R. 1973. Energetics of reproduction in birds. Pp. 78-107. *In* Breeding biology of birds (D. S. Farner, ed.), Natl. Acad. Sci., Washington, D. C.
- KLIMA, M. 1966. A study on diurnal activity rhythm in the European Pochard, *Aythya ferina* (L.), in nature. *Zool. Listy* 15:317-332.
- LASIEWSKI, R. C. AND W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13-23.
- LORENZ, K. 1953. Comparative studies on the behavior of the Anatinae. *Avic. Mag.* 57:157-182; 58:8-17, 61-72, 86-94, 172-184; 59:24-34, 80-91.
- MILNE, H. 1974. Breeding numbers and reproductive rate of eiders at the Sands of Forvie National Nature Reserve, Scotland. *Ibis* 116:135-152.
- ORIAN, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. *Ecol. Monogr.* 31:285-312.
- ORING, L. W. 1969. Summer biology of the Gadwall at Delta, Manitoba. *Wilson Bull.* 81:44-54.
- PRANGE, H. D. AND K. SCHMIDT-NIELSON. 1970. The metabolic cost of swimming in ducks. *J. Exp. Biol.* 53:763-777.
- SCHARTZ, R. L. AND J. L. ZIMMERMAN. 1971. The time and energy budget of the male Dickcissel (*Spiza americana*). *Condor* 73:65-76.
- SWANSON, G. A. AND A. B. SARCEANT. 1972. Observation of nighttime feeding behavior of ducks. *J. Wildl. Manage.* 36:959-961.
- TAMISIER, A. 1972. Rythmes nycthémeraux des sarcelles d'hiver pendant leur hivernage en Camargue. *Alauda* 40:235-256.
- TITMAN, R. D. 1973. The role of the pursuit flight in the breeding biology of the Mallard. Ph.D. thesis, Univ. of New Brunswick, Fredericton.
- VERNER, J. 1965. Time budget of the male Long-billed Marsh Wren during the breeding season. *Condor* 67:125-139.

- WIENS, J. A., S. G. MARTIN, W. R. HOLTHAUS, AND F. A. IWEN. 1970. Metronome timing in behavioral ecology studies. *Ecology* 51:350-352.
- WOLF, L. L. AND F. R. HAINSWORTH. 1971. Time and energy budgets of territorial hummingbirds. *Ecology* 52:980-988.

NORTHERN PRAIRIE WILDLIFE RESEARCH CENTER, JAMESTOWN, ND 58401.
ACCEPTED 10 JAN. 1975.

REQUEST FOR ASSISTANCE

Color-marked Swainson's Hawks.—Nestling Swainson's Hawks have been fitted with red, green, or blue vinyl patagial wing markers in the Columbia Basin of southcentral Washington. The markers are crescent shaped and will be visible on flying and perching birds. These markers will contain the symbol X or A followed by 2 numerals (e.g. X08, A23). Each hawk will have a single patagial marker on its right wing.

Post-fledging behavior, migration, and nest site selection are several of the more important points being studied.

Should you see any of these birds, please write—Richard Fitzner, Ecosystems Department, Battelle Northwest Laboratories, Richland, WA 99352. Include date, time of day, and location of the observation, plus name of observer(s), color of marker, and if possible, the numbers printed on the marker. Also include the number of Swainson's Hawks associated with the marked individual(s).